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Abstract (236 words)

A heterogeneous environment includes several levels of resource aggregation. Individuals do not respond in the same way to this heterogeneity depending on the scale at which they perceive it, and develop different foraging tactics accordingly. The development of methods to analyse animal movements has enabled the study of foraging tactics at several scales. Nevertheless, applied to large vertebrates, these methods have generally been used at large scales, such as for migration trips or the study of marine patches several kilometres large. In this study, we applied a recent method, the First-Passage Time analysis, based on a measure of the foraging effort along the path, to a much finer scale, i.e. under 500 meters. We used 30 daily paths of highly sedentary roe deer females. We modified the initial method, developed by Fauchald and Tveraa (2003), to detect a multi-patch use of the habitat. First-Passage Time analysis results showed that most of the female roe deer exploited their home range as a patchy resource, ranging from 1 to 5 areas of intensive use in their home range. These areas were identified as the most attractive sites within the roe deer female home range. Moreover, this method allowed us to rank the attractive areas according to the time spent in each area. Coupled with habitat selection analysis to identify what makes these areas attractive, the First-Passage Time analysis should offer a suitable tool for landscape ecology and management.

1. Introduction

Animals live in a patchy and hierarchical structured environment. Resources are aggregated and habitat complexity is generally reflected by this aggregation at different scales, lower levels nesting into upper levels (Kotliar & Wiens 1990). According to the scale, resources differ in density, turnover and predictability (Wu & Louks 1995, Fauchald 1999, Fauchald et al. 2000). The spatial and temporal distribution of a resource has a dominant influence on the searching efficiency and behaviour of a predator (Bell 1990). Hierarchical organization of resource aggregation thus induces both a differential perception of the habitat by predators according to the scale, and a modification of their search behaviour (Fauchald 1999). Animals will change their movement patterns in relation to changes in the spatial distribution of resources (Fritz et al. 2003). According to the Optimal Foraging Theory, when resources are distributed in patches, a consumer should increase its intake rate in a high resource density patch (Stephens & Krebs 1986), slowing down its speed and increasing its turning rate. Kareiva & Odell (1987) defined this concentration of consumer activity within an area of interest as an "Area-Restricted Search" behaviour (ARS). In fact, animal movement trajectories should result from the interaction between animal decisions and landscape properties (Morales et al. 2005).

Movement patterns of animals have mainly been analyzed using point distribution and path trajectories (Turchin 1998). Two main but different ways have been used to study vertebrate movements: studies based on random walks (Mårell et al. 2002) or on fractal dimension (Nams 2005). Correlated random walks have been used to model random movements with a certain degree of directionality (Kareiva & Shigesada 1983, Bergman et al. 2000), while the fractal dimension measures a path tortuosity. The tortuosity of foraging paths represents animal reactions to landscape heterogeneity in which animals translate environmental stimuli into movements (Crist et al. 1992, With 1994). Our understanding of

these relationships and processes has heavily relied on studies of small organisms or insects for which the monitoring of movement and the manipulation of the microlandscapes are feasible (e.g. Crist et al. 1992, With 1994, With et al. 1999). However, the monitoring of foraging paths of large animals has recently been developed (e.g. Gross et al. 1995, Etzenhouser et al. 1998, Viswanathan et al. 1999, Johnson et al. 2002, Mårell et al. 2002, Fauchald & Tveraa 2003, Fritz et al. 2003). The methods developed in these studies are mainly based on the shift between displacement patterns to define spatial scale changes. The study of trajectories allows the understanding of how the habitat heterogeneity affects foraging efficiency of the predators and how they react to changes in the spatial structure of resources.

In a recent study, Fauchald & Tveraa (2003) used variation in the search effort to assess at which scale consumers interact with their environment. The "First-Passage Time" (FPT) analysis, developed by Fauchald & Tveraa (2003), estimates the search effort, measuring the time spent by a predator to cross a circle of a given radius and so, highlights the part of the path where it adopts an ARS behaviour. The FPT analysis provides an estimation of the scale at which a consumer perceives resource by determining the exploited patch size (Fauchald & Tveraa 2003).

Determination of the perception scale of resource by an animal is important in understanding exploitation tactics, and this perception often differs from our own (Levin 1992). As most of the studies on large animal movements (e.g. Bascompte & Vilà 1997, Viswanathan et al. 1999, Bergman et al. 2000, Johnson et al. 2002, Mårell et al. 2002, Fritz et al. 2003, Austin et al. 2004), FPT analysis was performed on seabirds with high travelling abilities, making long foraging trips in low predictable resource habitats (Fauchald & Tveraa 2003, 2006, Pinaud & Weimerskirch 2005, 2007). However Frair et al. (2005) and Bailey & Thompson (2006) also performed FPT at a smaller scale, respectively on a large ungulate

(elk, *Cervus elaphus*) living in a more restricted home range and on groups of bottlenose dolphins (*Tursiops truncatus* Montagu) in a small surface area. In this study, we also attempted to apply the FPT analysis at a finer scale than in Fauchald & Tveraa (2003) and Pinaud & Weimerskirch (2005) in order to investigate the structure of roe deer (*Capreolus capreolus*) daily paths.

It has been assumed that herbivores generally feed at sites with high food quality and/or quantity, following qualitative predictions from Optimal Foraging Theory (e.g. Stephens & Krebs 1986). These predictions are supported by feeding-patch selection by deer which has been shown to be related to nutrient content and plant biomass (Wilmshurst & Fryxell 1995). Effects of habitat quality on roe deer population dynamics are quite well understood (Pettorelli et al. 2001, 2002, 2003a and b), but less so on the individual use of space (Mysterud et al. 1999). Though many studies on roe deer have been performed on the relationship between environmental factors and home range variation (Tufto et al. 1996, Mysterud et al. 1999, Saïd et al. 2005, Saïd & Servanty 2005), very few studies have investigated the heterogeneous use of the habitat within the home range.

In this paper, we used data from roe deer females equipped with GPS collars to investigate the structure of their movements throughout a day, using FPT analysis. Roe deer are known to have quite fixed and restricted home ranges (Strandgaard 1972, Liberg et al. 1998). It is thus particularly challenging to determine how roe deer may perceive or define the spatial organization of their resource in their daily environment and the impact of environmental structure on their movements.

The aim of our study was to see if roe deer perceive their habitat as heterogeneous. We hypothesized 1) that in a heterogeneous environment roe deer will use areas where they will increase their research of palatable plants and slow down their speed to increase their intake rate (Fauchald & Tveraa 2003); 2) roe deer will use several ARS throughout the day as this

species presents several activity phases with two main peaks at dawn and dusk (Bubenik 1960, Maublanc et al. 1991).

2. Methods

2.1. Study area

This study was carried out in the *Réserve Nationale de Chasse et de Faune Sauvage* of Chizé (see Figure 1). The Chizé reserve is an enclosed forest of 2614 ha in western France (46°05'N, 0°25'W). The elevation varies between 47 and 101 meters and the oceanic climate is characterized by mild winters and hot and dry summers. The Chizé forest includes three habitats contrasting in quality: an oak (*Quercus spp.*) forest with resource-rich coppices dominated by hornbeam (*Carpinus betulus*) in the north-eastern part, an oak forest with coppices of medium quality dominated by Montpellier maple (*Acer monspessulanum*) in the north-western part, and a poor beech (*Fagus sylvatica*) forest in the south part (Pettorelli et al. 2003a, Saïd & Servanty 2005; see Figure 1). The roe deer population at Chizé was estimated from Capture-Mark-Recapture methods to be approximately 400 adults in 2003 and 450 in 2004 (e.g. Gaillard et al. 1992, 1993, Pettorelli et al. 2002, 2003b, Gaillard unpubl. data).

2.2. Data collection

Does were equipped with Lotek's GPS_3300 radio collars (Lotek Wireless, Fish & Wildlife Monitoring). These collars, weighing 285 g, provided information on GPS positioning in differential mode (i.e., latitude, longitude, date and time) at pre-programmed intervals, fixed quality (DOP = dilution of precision) and ambient temperature. We scheduled collars programming one location every 5 minutes during 24 hours several days (1 to 3 days) per month. In September to December 2003, 2 females were equipped with GPS collars.

Then, in January-February 2004, 7 does were collared, in addition to the 2 previously equipped ones. Data location and data activity were recovered during the capture campaign in January-February 2004 and 2005. We obtained 15 daily paths with one point every 5 minutes from September 2003 to January 2004 and 15 daily paths from May to November 2004 (see Figure 2).

2.3. First-Passage Time analysis

The First-Passage Time method

To detect one or several ARS, we perform an FPT analysis on our data, following Fauchald & Tveraa's (2003) method, and using the software R (version 2.1.0; R Development Core Team 2005; Ihaka & Gentleman 1996) distributed under the GNU General Public License. The First-Passage Time (FPT) corresponds to the time needed by an animal to cross a circle of a given radius *r*. In order to perform the analysis, we assumed linear path with a constant speed between locations (e.g., Kareiva & Shigesada 1983) and completed inter-location path by points spaced every 5 meters as 90% of the path segments were longer than 5 meters. FPT was calculated at each point of individual paths for a given radius *r*, the location corresponding to the centre of the circle. We determined this measure of time for *r* ranging from 5 to 400 meters, as locations were spaced every 5 meters maximum and as the mean radius of the roe deer home range in the Chizé Forest is about 300 meters. The radius where the highest peak of variance in FPT is observed corresponds to the spatial scale (radius) of the area where the individual concentrates its search effort. We thus calculated the variance in FPT given by Var[log *t(r)*], *S(r)*, for each radius, and plotted it against the radius to obtain the spatial scale corresponding to the peak in *S(r), of the globality of individual path.* Spatial scale was confirmed when the plot of the FPT against time for the radius for which *S(r)* was maximum showed intensive search pattern, that is a high and constant FPT (see Fauchald &

Tveraa 2003, see Figure 3). Then, the intensive search area which corresponds to an ARS was identified on a path as the circle with the longest FPT for the determined spatial scale.

Multi-patch detection

Using the FPT analysis we detected the area where the search effort was the highest. Moreover, the circle radius gave us an estimation of the size of the exploited patch. However, the majority of our paths were clearly composed of more than one ARS (see Figure 2 and 3). The scale used to estimate the size of the main exploited patch can not be applied to the other ARS. Indeed, these ARS do not have necessarily the same radius than the one with the highest FPT. In order to assess the scale of these ARS, we need to remove the effect of the main ARS. We therefore modified the original process described by Fauchald & Tveraa (2003), and programmed by Pinaud & Weimerskirch (2005) to detect other potential ARS (program available contacting the authors). Part of the path included in the first determined FPT circle was removed and replaced by a segment that individuals cover in 5 minutes, as if the point before and after the ARS were really two successive points in the path. We then corrected the time of the locations following the removed path part. FPT analysis was finally performed on the modified path and we repeated the analysis until we obtained no more potential ARS (see Figure 4).

ARS validation

All circles for which the FPT plotted against time did not show any intensive search pattern were removed. Remaining circles were re-sorted: circles overlapping previously detected ARS and circles with radius less than 25 meters (GPS error calculated for Chizé forest = 25.56 ± 33.99 meters) were removed, especially in order to minimize the bias induced by the positioning error of the GPS. Finally, circles with a mean speed displacement higher

than the mean speed in the whole path were eliminated. Indeed, when applying the method in order to detect other ARS, the substitution of previously detected circles by a straight line covered in 5 minutes sometimes produced a bias in the detection. The identified parts of the path correspond to the parts where individuals spend more time and slow down their speed according to the ARS behaviour. As these parts of the path were substituted by a 5 minutes covered segment, the mean speed displacement along the path increased. A new ARS was detected where individual moved slower than the whole new generated path. However, the speed of the new generated path was higher than the one of the original path. The difference between the mean speed inside the ARS and the mean speed of the original path was smaller than with the generated path where the FPT method was applied. In extreme cases, speed inside the ARS was even higher than the speed of the original path and animals move faster in the detected circle than in the whole original path, that is not congruent with the definition of the ARS. Consequently, such circles were not taken into account. In order to identify these circles, we estimated the individual's mean speed in the ARS and compared it with the speed that the deer could have during the same time period. Given that the part of the path included in the circle is composed of *n* segments with associated speed, we randomly drew *n* segments, with replacement, of the whole path and estimated the mean speed. We performed this 100 000 times to obtain a mean speed distribution over the path. If the mean speed in the ARS was higher than the median value of the distribution, we did not take into account the corresponding circle. At last, the selected ARS were divided into 3 classes to assess whether the ARS differed according to the detection order: class 1, the first detected ARS; class 2, the second detected ARS; and class 3, the last ARS.

2.4. Statistical analysis

To test the effect of female identity, year, month, class of circle and circle radius as a covariable on the FPT in the circle, we fitted mixed linear models ("lme" function in the "nlme" R package, Laird & Ware 1982, Pinheiro & Bates 2000, Pinheiro et al. 2005) with the FPT in the circle, the year (2003 or 2004) as a two-modality fixed factor, the month (May, August, September, November and December) as a five-modality fixed factor, the class of circle (1, 2 or 3) as a three-modality fixed factor, and the females identity as random factor.

We did the same with the log-transformed FPT divided by the circle surface (FPT/m²). This measurement represents the utilization intensity of an area. We fitted mixed linear models with log(FPT/m²), year, month, class of circle (1, 2 or 3) as fixed factors, and only the females identity as random factor. We tested the random effect with a Restricted Maximum Likelihood (REML) procedure and the fixed effect with a Maximum Likelihood (ML) procedure (Vaida & Blanchard 2005). To select the best model, we used the Akaike Information Criterion (AIC) (Burnham & Anderson 1998) and we retained the model with the lowest AIC value. When the difference between two models was less than 2, we retained the simplest model according to the parsimony rules (Burnham & Anderson 1998). We checked the normality of residuals of our selected models for FPT (Shapiro-Wilk test: W = 0.994, p-value = 0.94) and log(FPT/m²) (Shapiro-Wilk test: W= 0.991, p-value = 0.77). Standard deviation of the random factor Female Id and the residuals were respectively for each model: Female Id SD = 0.852, Residual SD = 0.994, and Female Id SD = 0.517, Residual SD = 0.330.

3. Results

Over the 30 analyzed paths, 24 (13 in autumn/winter, 11 in spring/summer) presented a peak of the relative variance S(r) (See Figure 5) with a radius that seemed to correspond to an ARS. There was a total of 55 ARS detected (Class 1 = 23, Class 2 = 20, Class 3 = 12),

ranging from 1 to 5 ARS per path (mean = 2.2, SE = 0.96) (See Figure3). Radius of the detected circles ranged from 25 to 105 meters (mean = 50.1, SE = 20.47m), and the FPT ranged from 1h 38 min to 10h 05min (mean = 4h 13min, SE = 1h 59min). The best mixed linear model for the First-Passage Time included ARS radius (See Figure 6), circle class (See Figure 7) and month (See Figure 8), as well as the female ID (See Table1 and Table 2, AIC = 189.96). We observed a positive relationship between the FPT and the ARS radius (slope = 0.052, See Figure 6).

For log(FPT/m²), the best mixed linear model included circle class (See Figure 7), month (See Figure 8) and female ID (See Table 1 and Table 2, AIC = 75.36). Moreover, the result showed that log(FPT/m²) was negatively correlated with circle class: the use of the patches by the females was more intensive in the first detected ARS than in the second ones and the third ones (See Figure 7).

4. Discussion

Using the First-Passage Time analysis (Fauchald & Tveraa 2003), we detected at least one Area-Restricted Search behaviour (sensu Kareiva & Odell 1987) on most of the paths. Our study highlighted the existence of a second scale of landscape use which was finer than the home range scale for the roe deer (0.8 ha versus 24.5 ha for home range in Chizé forest (Saïd & Servanty 2005)). Many authors showed that certain portions within the home range are more frequently used than others (Adams & Davis 1967, Dixon & Chapman 1980, Springer 1982, MacDonald & Courtenay 1996). These areas of concentrated use by resident animals, loosely termed core areas, commonly include nest sites, daytime roost sites, refuges, and regions with the most dependable food sources (Burt 1943, Kaufmann 1962, Ford 1983).

Methods such as harmonic mean (Dixon & Chapman 1980) or bivariate models (Koeppl et al. 1975) were used to estimate core areas based on the cumulative proportion of an animal's location and the related increase of the area estimated by these locations within the total home range. We decided to use FPT method, because it allows identifying smaller sectors where animals spend more time using ARS than the core area method. Although the limited accuracy of the GPS collars did not allow us to explore nested levels of resource aggregation, our study highlights a patchy exploitation of their home range by the roe deer females. A large proportion of their activity is concentrated in restricted parts of their environment. In our study, we focused on the third scale of habitat selection defined by Johnson (1980; See Figure 9) but more accurate data are needed to highlight and define the finest scale (i.e., selection of food item inside feeding site).

The modification of the original method in order to detect further ARS along the path allowed us to highlight a multi-patch use of the home range at a daily level in roe deer females for 20 out the 24 paths. One major methodological questions associated with the use of our modified version of the FPT is obviously when to stop running the iterative analysis, i.e. how many patches make biological sense or can truly be distinguished with some statistical power. We chose to rely on a very simple and repeatable methodological rule to set our limit: we stopped when the size of the ARS circles fell below the accuracy of the GPS measures (i.e. below 25 m). There certainly are other decision rules, for instance for animals showing a very high selection for one or two patches, and for which the addition of another three minute circles, although significant, may not make much biological sense. We never had to question ourselves about this on our roe deer data, probably because our decision rule fell nicely within the scales at which roe deer make decisions about patch choices. However, we encourage users of this modified method to adapt the decisions rules to their equipment but more so to the biology of their studied animals.

In our study, we used the First-Passage Time value (FPT) and the FPT by surface unit. The first one represents the time an individual stayed in the patch and gives us the time he spent foraging. The second one represents the exploitation effort of an individual in a patch. It indicates the intensity with which an individual foraged in the patch. We found a continuum in the FPT between the circle classes: animals spent more time in circles of first class than in circles of second and third classes. However, this result can be directly linked to the way our extension of the FPT method works. Indeed, as the method focuses on the ARS where the FPT is the maximum, the first detected ARS is systematically the one with the highest FPT, the second detected ARS is the one with the second highest FPT and so on. Nevertheless, the exploitation intensity ($\log(FPT/m^2)$) of the patch really differs between circle classes. The time spent in an ARS of a given radius is higher in circles of the first class than in circles of the two other classes. Thus, the detection order seems to reflect an order of preference in the use of patches within the home range and roe deer should spend more time in the most valuable patch.

There could be another way to interpret differences between circle classes. They could reflect a spatial discrimination of different behaviours (e.g., resting and feeding activities) that imply different constraints and resources, or environmental features. In Fauchald & Tveraa (2003, 2006) and Pinaud & Weimerskirch (2005), studied paths were foraging trips. They performed respectively the FPT analysis on the Antarctic petrel (*Thalassoica antarctica*) and the yellow-nosed albatross (*Thalassarche carteri*) during the breeding period. In Pinaud & Weimerskirch (2007), the analysis was also performed on seven breeding species of Procellariforms. During this period, the two species display a central-place forager behaviour (Ashmole 1971): they make a long foraging trip of several days after they left the colony, and then come back. Birds thus have to maximize their energy gain, spending most of their trip in the food patch so that their activity within the ARS is mainly related to foraging. In our study,

like in Frair et al.'s (2005) study, roe deer path did not seem to be typically displaying central-place foraging as starting point hours were chosen arbitrarily and the path remained all the day including feeding and resting activity for which roe deer look for different structures of vegetation (Mysterud & Øtsbye 1995). Frair et al. (2005) worked at a large temporal scale using elk (*Cervus elaphus*) paths taken over several months with a 2 hour inter-location interval. They used the FPT analysis to define 3 scales of movements (inter-patch relocations, foraging displacements and resting movements). In our study we used daily paths, working at a finer temporal scale with a 5 minutes inter-location interval. Performing the FPT analysis on paths with locations every 5 minutes gives us a sharp information of the animal movement and allows us to highlight a succession of used patches at the scale of the day. These patches can also be characterized by activity data, as GPS collars can be used in combination with activity sensors (e.g. Adrados et al. 2003, Frair et al. 2005). The use of such tools to identify activity within FPT circles will provide means to assess whether animals display a multi-patch use of the environment because of the resource patch heterogeneity, versus a spatial discrimination between different behaviours (e.g. resting vs feeding sites).

The patch use behaviour reported in this study corresponds, in the case of a food search strategy, to the animal's perceptions of the resource aggregation, and it is probably related to the habitat heterogeneity. This habitat heterogeneity, natural or due to human disturbance, drives ecological processes (Fortin & Agrawal 2005). Understanding the link between these processes and the heterogeneity of the environment is a key question for management and landscape ecology (Wiens et al. 1993). Coupling a Geographic Information System with the FPT analysis would allow us to characterize areas of interest (eg. ARS for feeding, resting site) in terms of environmental features (topography, vegetal cover, thermic cover, vegetation quality) according to animal activity. FPT analyses should offer a suitable tool to be incorporated in habitat selection analysis in order to improve identification of the

environmental features that make a habitat attractive to animals. Fine approaches as FPT analysis enable to highlight the response of species to habitat heterogeneity at very small scales. The study of this behavioural response allows assessing in a finest way the consequences of management decisions on population dynamics and then to orientate these decisions to improve the management of these populations and their habitats.

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Figure legends:

Figure 1: Spatial representation of the Chizé reserve (2614 ha), an enclosed forest in western France. Daily path of female roe deer in 2003 is also represented.

Figure 2: Example of a path where several areas were detected (female 35, the 24th of November 2003). The numbers beside the circle correspond to the detection order of the areas. The circle 1 is a first class circle and the circle 2 a second class circle. The arrows indicate the direction of the walk.

Figure 3: Example of First-Passage Time all along the path for the scale assessed by the analysis (here 50 meters; female 35, the 30th of December 2003). The high and constant FPT near dawn corresponds to the most intensive Area-Restricted Search behaviour. A second one near dusk, lower, seems to indicate a multi-patch use of the environment throughout the day.

Figure 4: Example of detection of a second area: (a) a first circle was detected after the FPT analysis was performed; (b) part of the path inside the first detected circle was removed and replaced by a segment the individual covered in 5 minutes; (c) FPT analysis was performed again and the second area was detected.

Figure 5: Mean variance in First-Passage Time S(r) against the radius r of all paths showing ARS and example for 3 paths. The peak in S(r) corresponds to the used spatial scale. Roe deer female F34 does not express ARS in May 2004 (according to Pinaud & Weimerskirch 2005).

Figure 6: First-Passage Time (Hours) as a function of the corresponding radius (meters) of detected areas.

Figure 7: First-Passage Time (Hours) (empty box whisker plots) and Mean log(First-Passage Time / Surface Unit) (log(FPT/m^2)) (full box whisker plots) according to the circle classes. The First-Passage Time decreased with the detection order (class 1 vs class 2: df = 38, t-value = -4.897, p-value < 0.001; class 1 vs class 3: df = 38, t-value = -5.035, p-value < 0.001; class 2 vs class 3: df = 38, t-value = -1.289, p-value = 0.205). The log(FPT/m^2) decreased with the

detection order (class 1 vs class 2: df = 38, t-value = --6.039, p-value < 0.001; class 1 vs class 3: df = 38, t-value = -7.017, p-value < 0.001; class 2 vs class 3: df = 38, t-value = -2.432, p-value = 0.020).

Figure 8: First-Passage Time (Hours) (empty box whisker plots) and Mean log(First-Passage Time / Surface Unit) (log(FPT/m²)) (full box whisker plots) according to the month.

Figure 9: The four scales of habitat selection defined by Johnson (1980), with radius in meters in the case of roe deer. The first corresponds to the selection of the repartition area of the species; the second one corresponds to the selection of the home range; the third one corresponds to the selection of the feeding sites inside the home range; and the last one corresponds to the selection of the alimentary items inside the feeding site.

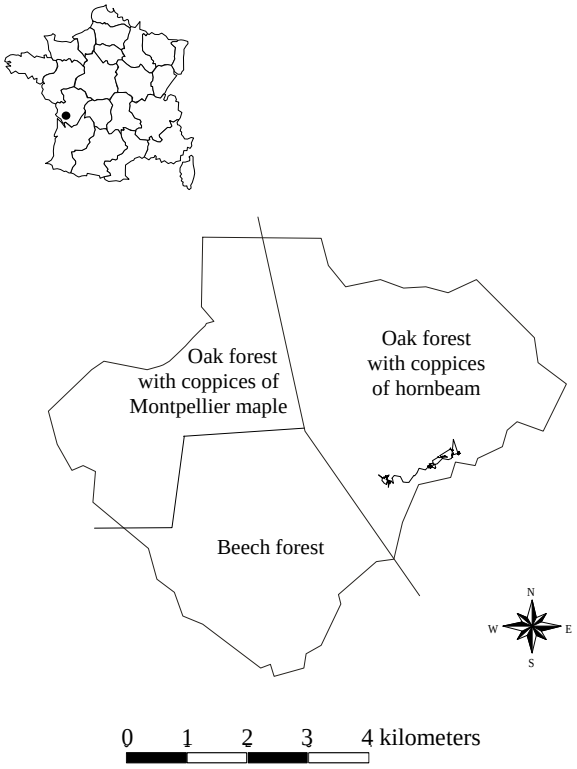
Table 1. Results of the mixed linear models for the First-Passage Time and for the log-transformed First-Passage Time divided by the circle area of female roe deer paths in Chizé forest, with the female identity as random factor.

Tested models Response variable	Random effect	Fixed effect	Number of Parameters	Δ AIC
First-Passage Time	Female	Month	2	52.65
		Year	2	48.58
		Constant	1	46.54
		Circle Class + Month	3	39.13
		Circle Class + Year	3	34.56
		Circle Class	2	32.57
		Radius	2	29.61
		Radius + Circle Class + Year	4	7.34
		Radius + Circle Class	3	6.02
		Radius + Circle Class + Month	4	0
log(First-Passage Time/ Surface unit)	Female	Year	2	41.61
		Year + Circle Class	3	31.67
		Circle Class	2	29.99
		Month	2	15.28
		Month + Circle Class	3	0

Table 2. Estimates for the mixed linear models selected in table 1 for the First-Passage Time and for the log-transformed First-Passage Time divided by the circle area of female roe deer paths in Chizé forest, with the female identity as random factor. Standard deviation of random factors are respectively for each model: Female Identify SD = 0.852, Residual SD = 0.994, and: Female Identify SD = 0.517, Residual SD = 0.330.

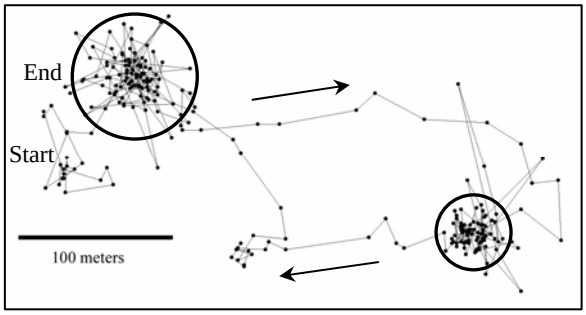
Response variable	Tested models	Explanatory Variables	Value	S.E	D.F	t-value	p-value
First-Passage Time	Radius + Circle Class + Month	(Intercept)	+1.42	0.762	38	+1.864	0.070
		Radius	+0.08	0.010	38	+7.539	<0.001
		Circle Class 2	-1.66	0.339	38	-4.895	<0.001
		Circle Class 3	-2.24	0.444	38	-5.032	<0.001
		May	-0.42	0.622	38	-0.674	0.505
		August	+0.06	0.719	38	+0.081	0.936
		October	+0.24	0.784	38	+0.303	0.764
		November	+0.50	0.804	38	+0.621	0.539
		December	-1.67	0.732	38	-2.274	0.029
log(First-Passage Time/ Surface unit)	Circle Class + Month	(Intercept)	-7.18	0.251	39	-28.626	<0.001
		Circle Class 2	-0.46	0.111	39	-4.178	<0.001
		Circle Class 3	-0.50	0.146	39	-3.418	0.002
		May	-0.37	0.238	39	-1.562	0.126
		August	+0.42	0.248	39	+1.706	0.096
		October	+0.15	0.279	39	+0.523	0.604
		November	+0.03	0.287	39	+0.121	0.905
		December	-0.78	0.259	39	-3.017	0.005

Fig.1


Oak forest
with coppices of
Montpellier maple
Oak forest
with coppices
of hornbeam
Beech forest
N
W
E
S
0 1 2 3 4 kilometers

1 **Fig.2**

2



1 **Fig.3**

2

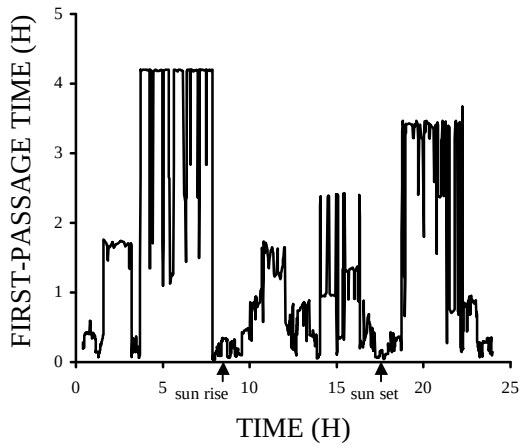

FIRST-PASSAGE TIME (H)
0
1
2
3
4
5
0
5
sun rise
10
15
sun set
20
25
TIME (H)

Fig.4

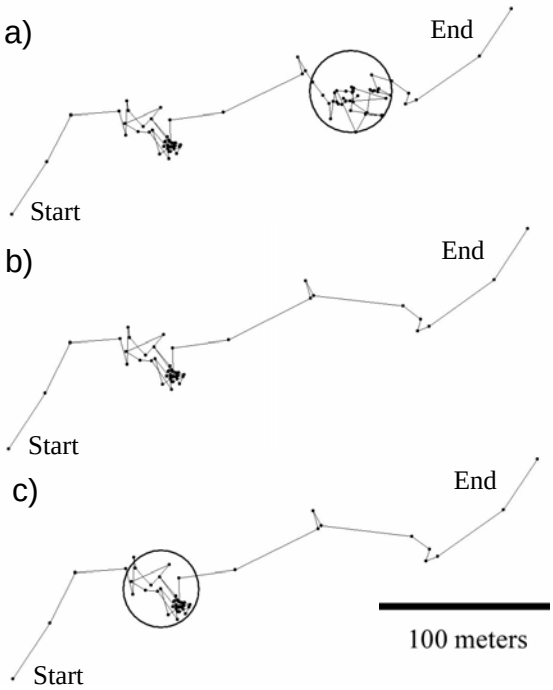
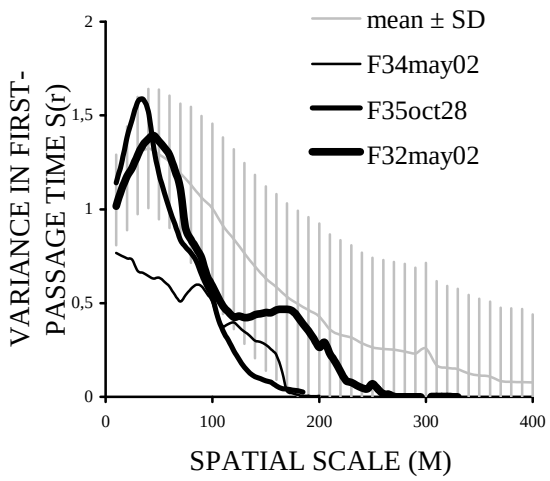
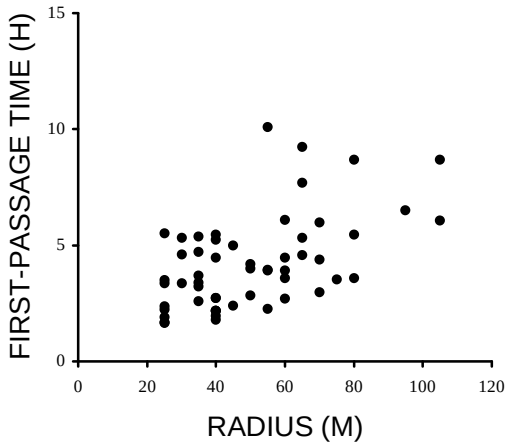


Fig.5


mean ± SD
F34may02
F35oct28
F32may02
VARIANCE IN FIRST-PASSAGE TIME S(r)
SPATIAL SCALE (M)
0
0,5
1
1,5
2
0
100
200
300
400

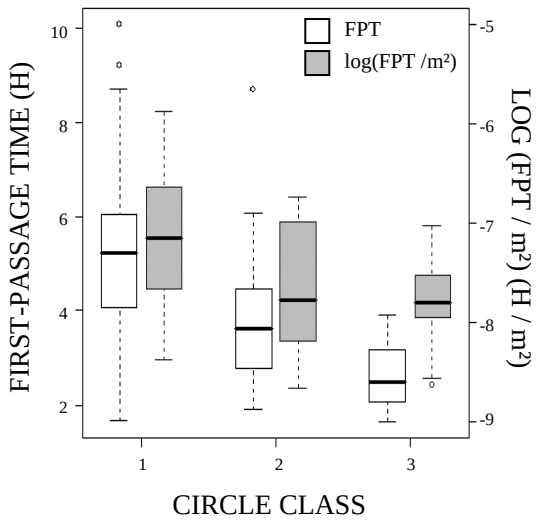
1 **Fig.6**

2



3

Fig.7


FPT
log(FPT /m²)
FIRST-PASSAGE TIME (H)
LOG (FPT / m²) (H / m²)
CIRCLE CLASS
10
8
6
4
2
-5
-6
-7
-8
-9
1
2
3

1 **Fig.8**

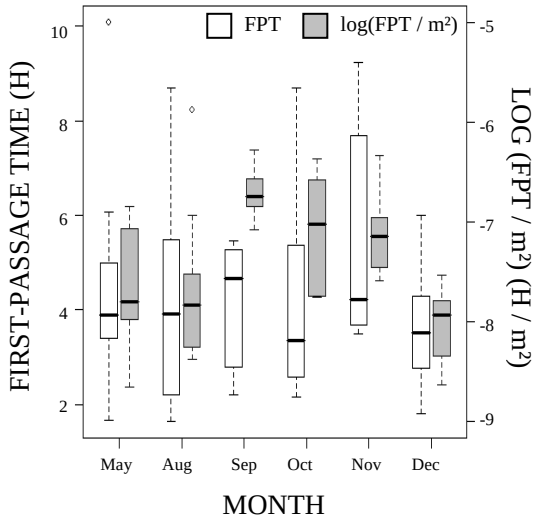
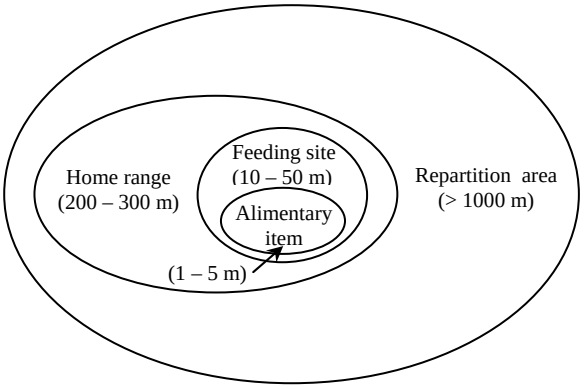

FPT
log(FPT / m²)
FIRST-PASSAGE TIME (H)
LOG (FPT / m²) (H / m²)
10
8
6
4
2
-5
-6
-7
-8
-9
May
Aug
Sep
Oct
Nov
Dec
MONTH

Fig.9


Home range
(200 – 300 m)
Feeding site
(10 – 50 m)
Alimentary
item
(1 – 5 m)
Repartition area
(> 1000 m)